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Origins and evolution of cinnamon and camphor: A phylogenetic and historical biogeographical analysis of the *Cinnamomum* group (Lauraceae) ☆

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ABSTRACT

Tropical and subtropical amphi-Pacific disjunction is among the most fascinating distribution patterns, but received little attention. Here we use the fossil-rich *Cinnamomum* group, a primarily tropical and subtropical Asian lineage with some species distributed in Neotropics, Australasia and Africa to shed light upon this disjunction pattern. Phylogenetic and biogeographic analyses were carried out using sequences of three nuclear loci from 94 *Cinnamomum* group and 13 outgroup samples. Results show that although there are three clades within a monophyletic *Cinnamomum* group, *Cinnamomum* and previously recognized subdivisions within this genus were all rejected as natural groups. The *Cinnamomum* group appears to have originated in the widespread boreotropical paleoflora of Laurasia during the early Eocene (ca. 55 Ma). The formation and breakup of the boreotropics seems to have then played a key role in the formation of intercontinental disjunctions within the *Cinnamomum* group. The first cooling interval (50–48 Ma) in the late early Eocene resulted in a floristic discontinuity between Eurasia and North America causing the tropical and subtropical amphi-Pacific disjunction. The second cooling interval in the mid-Eocene (42–38 Ma) resulted in the fragmentation of the boreotropics within Eurasia, leading to an African–Asian disjunction. Multiple dispersal events from North into South America occurred from the early Eocene to late Miocene and a single migration event from Asia into Australia appears to have occurred in the early Miocene.

1. Introduction

The occurrence of intercontinental disjunctions in the natural geographic ranges of many seed-plant groups has long fascinated biologists (Raven, 1972; Thorne, 1972), with 16 categories of intercontinental disjunction recognized by Thorne (1972). Among them, the amphi-Pacific tropical disjunction is applied to plants that are distributed in tropical regions on both sides of the Pacific Basin with the highest plant diversity on Earth (Thorne, 1972; Raven, 1988). However, this disjunction pattern has received relatively little attention, compared to the more extensively studied eastern Asian–North American disjunction (Li et al., 2011; Li and Wen, 2013).

In order to explain the amphi-Pacific tropical disjunction, multiple hypotheses and plausible migration pathways have been postulated. Among them, that there was a continuous boreotropical paleoflora during the climatically warm periods of the Paleogene in the Northern Hemisphere (Wolfe, 1975; Tiffney, 1985). Evidence for this biome has been supported by molecular analysis for a number of plant groups, including Amaryllidaceae (Meerow

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et al., 1999), Annonaceae (Couvreur et al., 2011; Erkens et al., 2009, 2012), Fabaceae (Lavin and Luckow, 1993; Lavin et al., 2005), Lauraceae (Chanderbali et al., 2001; Li et al., 2011), Magnoliaceae (Azuma et al., 2001) and Malpighiaceae (Davis et al., 2002b, 2005), as well as animal groups like Cladocera (Van Damme and Sinev, 2013).

The Bering and North Atlantic land bridges have been used to explain the migration of subtropical and tropical lineages in the context of the boreotropics hypothesis (e.g. Tiffney, 1985; Davis et al., 2002a; Li et al., 2011) and van Steenis (1962) postulated various transoceanic land bridges to account for the amphi-Pacific disjunctions of many plant genera. Long-distance dispersal may also play a significant role in disjunct tropical genera with fleshy fruits, or fruits that can float and remain viable for a longer time in salt water (Thorne, 1972; Raven and Axelrod, 1974; Givnish and Renner, 2004). Testing these competing hypotheses and dispersal pathways is important for understanding the origins of these intercontinental disjunction patterns.

The *Cinnamomum* group, as proposed by Chanderbali et al. (2001), is a subset of the tribe Cinnamomeae (Lauraceae) ranging from tropical and subtropical Asia, Australia and Pacific Islands, to tropical America and Africa. As defined currently, it contains more than 350 species represented by the genera *Aiouea* Aubl., *Cinnamomum* Schaeff., *Mocinnodaphne* Lorea-Hern. and the species of *Ocotea ikonyokpe* van der Werff. Phylogenetic analysis of ITS sequence data unexpectedly placed the African *O. ikonyokpe* within the *Cinnamomum* group, rather than the remainder of the genus *Ocotea* Aubl. (Chanderbali et al., 2001). Described by van der Werff (1996) from Cameroon, *O. ikonyokpe* is the only African element within the *Cinnamomum* group, which otherwise has a tropical and subtropical amphi-Pacific disjunct distribution.

Cinnamomum with ca. 350 spp. (Rohwer, 1993), comprises the bulk of the *Cinnamomum* group and occurs in subtropical and tropical regions on both sides of the Pacific Basin. Its members have long been recognized for their economic importance as the sources of camphor, spices, phytomedicines and high quality wood (Wijesekera et al., 1975; Farrell, 1985; Loi, 1996; Ravindran et al., 2003). In addition, as conspicuous elements of tropical and subtropical evergreen broad-leaved forests, *Cinnamomum* species are also ecologically important (Lin, 1965; Kira, 1991; Wang et al., 2007). Tropical Asia is the most significant center of *Cinnamomum* species diversity, followed by the Neotropics with a further ca. 47 species (Lorea-Hernández, 1996). The Asian *Cinnamomum* species are divided traditionally into two sections based on morphological traits such as leaf arrangement, leaf venation pattern, presence or absence of perulate buds or domatia: sect. *Camphora* Meissn. and sect. *Cinnamomum*. Based on similar grounds, all the five Australian native *Cinnamomum* species have been placed in sect. *Cinnamomum* (Hyland, 1989). However, unlike the Asian and Australian species, Neotropical *Cinnamomum* species present a mixture of the characters found in the two Asian sections (Lorea-Hernández, 1996). Most of the Neotropical species currently included in *Cinnamomum* had originally been described in *Phoebe* Nees, but were transferred to *Cinnamomum* by Kostermans (1961). The affinity between Neotropical *Phoebe* and Asian *Cinnamomum* species has been noted previously by Nees von Esenbeck (1836) and Meissner (1864), who created *Phoebe* subgenus *Persoideae* Meisn. for the Asian species and subgenus *Cinnamoideae* Meisn. for the American ones.

The question of whether *Cinnamomum* is monophyletic has been ongoing and 35 years after Kostermans (1961), the Neotropical species of *Cinnamomum* were revised by Lorea-Hernández (1996), with 47 species accepted. Based on a cladistic analysis of 36 morphological features for Lauraceae genera, Neotropical *Cinnamomum* species are more closely related to Asian *Cinnamomum* species than to *Phoebe* (Lorea-Hernández, 1996). In contrast, a molecular phylogenetic study of the family by Chanderbali et al. (2001) showed that the Neotropical *Cinnamomum* species included in their analysis formed a clade with *Aiouea dubia* Mez, *A. guianensis* Aubl. and *Mocinnodaphne cinnamomoidea* Lorea-Hern., rather than forming a monophyletic group with the Asian *Cinnamomum* species. However, forcing monophyly of *Cinnamomum* and its allies added just one extra step in the maximum parsimony analysis (see Figs. 3 and 4 in Chanderbali et al., 2001), suggesting that branch support was potentially weak or strongly character dependent.

The monotypic Mexican genus *Mocinnodaphne* was described by Lorea-Hernández (1995) and separated from genera such as *Cinnamomum*, *Ocotea*, *Nectandra* Rolander ex Rottb. based on the reduction in number of fertile staminal whorls. *Aiouea*, with ca. 20 species (Renner, 1982), was not supported as monophyletic by either morphological (Penagos, 2010) or molecular data (Chanderbali et al., 2001) and of the three *Aiouea* species sequenced by Chanderbali et al. (2001), two were nested within the Neotropical *Cinnamomum* clade and one in the genus *Ocotea*.

Cinnamomum has an abundant and widespread fossil record and has been reported from the Upper Cretaceous of Asia (Guo, 1979), Europe (Coiffard et al., 2008), North America (e.g. Berry, 1929; Bell, 1957, 1963; Lozinsky et al., 1984; Crabtree, 1987; van Boskirk, 1998; Johnson, 2002) and Australasia (von Ettingshausen, 1883, 1887a,b, 1891; Pole, 1992; Cantrill et al., 2011), making the geographical origin of the genus uncertain. Its Cenozoic diversity reached the climax in the Eocene, gradually decreasing from the Oligocene to Miocene (Berry, 1916). Though numerous fossil records should make the *Cinnamomum* group a desired target to explore the origins of its amphi-Pacific disjunction pattern, the majority of the fossils attributed to *Cinnamomum*, especially the 19th and early 20th Century determinations, is based purely on superficial similarities of venation features and are not conclusive.

Previous studies have revealed that cpDNA makers are of limited use for reconstructing phylogenetic relationships in Lauraceae, particularly for the Perseeae–Laureae clades (Rohwer, 2000; Chanderbali et al., 2001; Rohwer and Rudolph, 2005; Fijridiyanto and Murakami, 2009; Rohwer et al., 2009; Li et al., 2011). Therefore for this study, we selected three nuclear markers, ITS and two low-copy nuclear genes (*LEAFY* and *RPB2*), based on results of the above-mentioned studies to resolve phylogenetic relationships within the *Cinnamomum* group along with a significant increase in taxon sampling. Accordingly, the main objectives of this study were to

(1) reconstruct phylogenetic relationships within the *Cinnamomum* group and elucidate if the group, the genus *Cinnamomum* and previously recognized subdivisions within it are monophyletic;
(2) explore the biogeographic history of the *Cinnamomum* group and elucidate the origin and nature of its amphi-Pacific and other disjunctions, including the tropical North and South American disjunction, the African–Asian disjunction and the disjunction between Asia and Australia.

2. Materials and methods

2.1. Taxon sampling

A total of 94 accessions for 76 species in the *Cinnamomum* group were included (Supplementary Table S1), covering nearly the entire distribution range of the group. ITS sequences deposited in Genbank were downloaded for four Neotropical *Cinnamomum* group species and the African *O. ikonyokpe*. Five *Persea* group and eight core Laureae species were selected as outgroups based on previous studies (Chanderbali et al., 2001; Li et al., 2011) which